The threat of alien invasive grasses to lowland Cape floral diversity: an empirical appraisal of the effectiveness of practical control strategies

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EUROPEAN ANNUAL GRASSES IN HIGHLY fragmented natural ecosystems along the South African west coast are displacing wildflowers, which form the basis of a growing lucrative, nature-based tourist industry. We examined the cost-effectiveness of different labour-intensive strategies linked to a national poverty relief programme for controlling invasive annual grasses in renosterveld. The treatments tested involved combinations of grass mowing, hand-clearing, light and intense burning and pre-emergent herbicide application randomized over forty-eight 100-m^2 plots in the Tienie Versfeld Wildflower Reserve. Springtime vegetation responses were monitored over two successive years; labour, capital equipment and consumable costs were audited. Total clearing costs associated with intense burning of uncut grass (R415/ha), grass mowing (R924/ha) and light intensity burning of mowed grass (R1338/ha) were all less than those (up to R1 927/ha) reported for clearing dense stands of woody aliens. However, costs of hand-clearing of grass (R6 743/ha) and pre-emergent herbicide application (R13 380/ha) were much greater. Intense burning, the cheapest strategy overall, was ineffective as this promoted recruitment of both alien invasive annual and perennial grasses and inhibited recruitment of native geophytes. We conclude that mowing of grass-infested renosterveld prior to grass seed maturation, and the removal of the cut grass biomass for use as fodder in restricted feed lots to offset clearing costs, provides the most credible strategy for controlling the annual grass populations to conserve native floral diversity over the short term.

Introduction

Grasses are one set of invasive species that collectively threaten regional and even global aspects of ecosystem function.[1,2] Numerous examples of alien grass invasions are found on all continents, though large-scale invasions are less common in Eurasia and Africa, where much of the tropical areas are covered by so-called derived grasslands and savannas. These are presumed to be formerly forested areas in which grasses now dominate as a consequence of intense ungulate grazing and a long history of human activity. This is especially pertinent in Africa, where grasses have evolved with hominids for millions of years. Their adaptations to severe grazing, which include rapid growth response to defoliation and subterranean vegetative propagating organs, also confer resistance to fire. Therefore, it is not unexpected that Africa, and to a lesser extent Asia, have been donors rather than recipients of fire-adapted alien grasses. Despite this propensity, there are examples in Africa of large-scale recipient invasions by alien grasses from other continents, or from other areas within the continent. These include the establishment of several European annual grasses in Mediterranean climate regions of South Africa and the recent spread of perennial grasses of South American, Central and North African origin in southern Africa.[3] These alien grasses are known to impact on ecosystem structure, function and resources by accelerating wild fires, decreasing floral and faunal diversity and forage stability, altering soil food webs, soil moisture dynamics and decomposition cycles.[4–6] Much of this knowledge has been derived from studies outside South Africa with limited information available on local impacts.[3]

Along the west coast of South Africa the displacement of the natural vegetation by alien grasses is emerging as a potential cause for concern, especially in terms of the wildflower diversity, which forms the basis of a growing lucrative, nature-based tourist industry in a Mediterranean-climate region unique in terms of its rich floristic diversity and endemism.[7] Evidence that the natural flora in this region, which is listed among 25 global biodiversity hot spots,[8] is under threat from competition by alien grasses is based on an apparent recent increase in the abundance of especially annual grasses on bottomlands and plains.[9,10] This advance of annual grasses into natural landscapes, particularly from contaminated road verges and agricultural lands, is facilitated through the transport of their seeds on the hide of grazing animals,[2,11] and in the dung of domestic livestock and wildlife.[12–14] It is exacerbated by rangeland deterioration caused by ploughing, vegetation clearing and burning, by soil nutrient enrichment from fertilizer run-off and nitrogen-fixing leguminous species,[3] and by grazing that tends to be more intensive in small habitat fragments.[15,16]

As on other continents,[6,17] negative correlations between the density of alien invasive annual grasses and herbaceous wildflower diversity have been reported in southern Africa, both in lowland fynbos and succulent Karoo ecosystems.[9,10] In response to these threats to the natural biodiversity, local landowners in these popular nature tourist ecosystems are attempting to control the problem grasses, the identities and distributions of many of which are still unknown, by the application of herbicides and intensive grazing by domestic livestock during the winter growing season. Should this problem reach the level of alien woody plant invasions experienced elsewhere in the region, local economies in already poorly resourced communities could be seriously undermined.[18]

An appropriate and viable management solution to the problem of alien grass invasion is needed. A scientific analysis of the situation should inform the correct management policy and channelling of resources to counter the negative impacts of this invasion. Given the high levels of unemployment in the region, a labour-intensive experimental approach would have two advantages. First, it would provide employment on a medium-term basis while empirical data are being generated. Second, it would provide local communities with an opportunity to become involved in a science-based approach to land management. The latter, through linkage to local schools and adult education programmes, could assist in raising environmental awareness in the region, a necessary condition for sustainable development. Funding is accessible from the Working for Water programme, with an annual budget of about US$60 million (R400 million), whose dual purpose is the protection of South African water resources by controlling alien invasive plants and job creation through employment of impoverished local people in control projects.[19] In view of these advantages, we empirically examined the cost-effectiveness of different practical strategies involving local communities for managing invasive grass infestations in a west coast reserve.

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Methods and materials

Study site

The study site was the 20-ha Tienie Versfeld Wildflower Reserve (33°20′18″S, 18°16′12″E), situated between the towns of Yzerfontein and Darling approximately 80 km north of Cape Town. The reserve originally formed part of the farm 'Slangkop' owned by the Versfeld family of Darling, but administered since 1956 by the South African National Biodiversity Institute. The reserve's natural flora is renosterveld, broadly categorized as evergreen fire-prone vegetation lacking Proteaceae and Ericaceae, which is dominated by small-leafed asteraceous shrubs, especially *Elytropappus rhinocerotis* (L.f.) Lees (renosterbos or rhinoceros bush), with an understorey of Poacaeae (grasses) and geophytes.[20,21] Renosterveld is ecotonal to fynbos and succulent Karoo, occurring on moderately fertile, clay-rich (shale and granite derived) soils on lower mountain slopes, interior valleys and coastal forelands at annual precipitation levels between 300 and 600 mm. Fynbos develops under this rainfall on oligotrophic soils, and succulent Karoo replaces renosterveld on fertile soils under drier conditions. Post-colonial firewood collection, and burning and grazing of vegetation are thought to have shaped modern renosterveld by transforming a woody shrubland-perennial grassland mosaic into a more uniform shrubland dominated by *E. rhinocerotis,* other pyrophillic shrubs and more recently by alien invasive annual grasses.[21,22] Historical records indicate that the reserve was never ploughed, though it has been used for grazing by cattle, apparently to regulate the alien invasive grass infestations originating from the surrounding wheat lands. during our study, however, cattle were excluded from the reserve.

The principal alien species of invasive annual grasses in the reserve include *Lolium multiflorum* Lam. or hybrids (rye grass), which in 1659 was the first species to be proclaimed a weed in South Africa,[23] *Avena fatua* L. (wild oats) and *Bromus diandrus* Roth. (ripgut), most abundant in marshy areas along a drainage line in the centre of the reserve, and *Hordeum murinum* L. (mouse barley), which occurs most frequently in disturbed areas along the reserve's northern boundary previously excavated for the laying of a pipeline. The principal alien species of perennial grasses include *Cynodon dactylon* (L.) Pers. (kweek), widespread throughout the reserve, and *Pennisetum clandestinum* Chiov. (kikuyu), restricted to the fence line along the reserve's southern boundary.

Project financing and implementation

A local contractor, comprising one supervisor and 15 workers, was hired for a period of 15 days in early autumn (March) of 2003. Capital equipment (mechanized brush cutters, herbicide applicators, fuel drums, spades, rakes, pitchforks, protective gear, etc.) and consumables (fuel, filters, blades, herbicides, etc.) required for the mechanical and chemical manipulation of the alien invasive grass infestations were purchased. One day was spent training the workers in the correct use of the various implements and in the proper adherence to safety protocols.

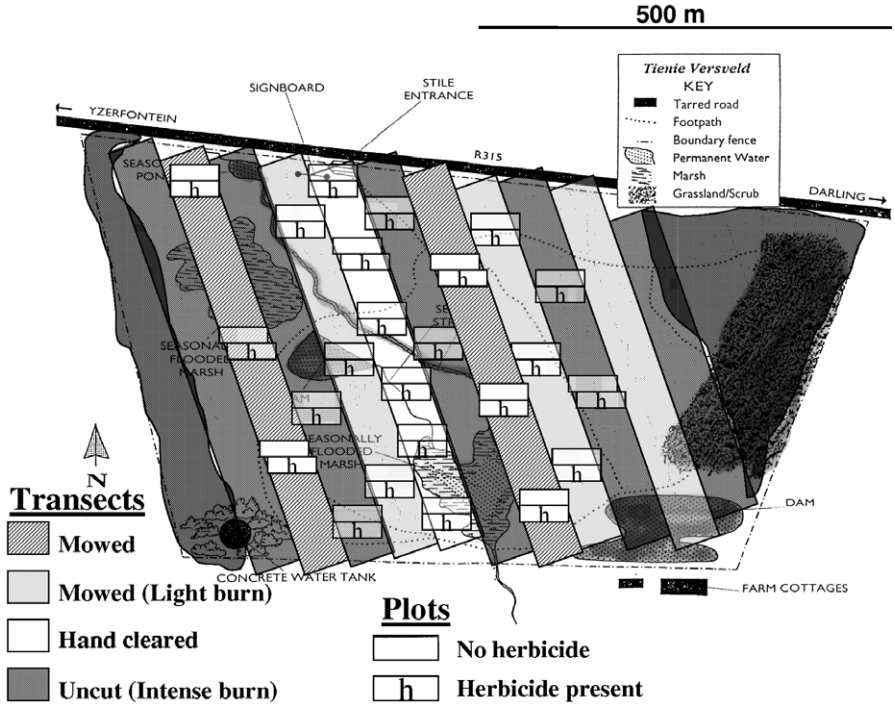

Fig. 1. Schematic illustration of layout of differently treated experimental transects and plots in the Tienie Versfeld Wildflower Reserve.

Experimental treatments

Parallel 10 000-m^2 (500 m long × 20 m wide) transects, orientated in a north–south direction, were marked out in the reserve in the early autumn of 2003 (Fig. 1). All grasses were completely removed (hand-cleared) from the middle transect through the reserve's centre and the hand-harvested grass biomass deposited and uniformly spread in an adjacent undisturbed transect. In the remaining transects, the grass was brush cut (mowed) to a height of about 5 cm in alternate transects and the cut grass biomass also deposited and uniformly spread in adjacent uncut transects. The deposition of the hand-harvested and cut grass biomass effectively doubled the accumulated lifeless grass litter in the undisturbed transects, with subsequent fire intensities presumably increased in proportion to the enhanced fuel load. Following grass clearing and mowing, a 20-m-wide fire-break was brush cut around the reserve's perimeter and all the vegetation in the reserve, with the exception of that in two 10 000-m^2 mowed transects, burnt with the assistance of the operational fire management team of the Western Cape Nature Conservation Board. These mechanical manipulations provided four primary treatments, namely, hand-cleared, mowed, lightly burnt (brush-cut with a low fuel load), and intensely burnt (uncut with a high fuel load). Undisturbed (uncut and unburned) controls were excluded from the experimental design because the intention was to compare only the relative influence of the different manipulations on the performance of alien invasive grasses and native vegetation.

Forty-eight 100-m^2 experimental plots (20 m long × 5 m wide) were randomized within the 10 000-m^2 transects representing the four primary treatments, their placement avoiding marshy (seasonally inundated) areas (Fig. 1). There were 12 experimental plots per primary treatment. In half of the experimental plots randomized within the four primary treatments (24 plots overall), a secondary chemical manipulation was applied (Fig. 1). This constituted the addition of a pre-emergent herbicide (Snapshot, Dow Agro-Sciences), whose active ingredients (trifluralin and isoxaban) were administered at a dosage of 2.5 kg per 100 m^2.

Vegetation measurements

The abundances of the native and alien grass, herbaceous and woody species present in the 48 × 100-m^2 experimental plots were measured towards the end of the winter rainy season in mid-spring (October) in two successive observation years that received different absolute amounts of annual precipitation, namely, 302 mm in 2003 and 439 mm in 2004. These precipitation amounts, obtained from a meteorological station (Langebaanweg: 33°05′S, 18°02′E) close to the experimental site, exceeded the documented 48-year average of 253 mm by 19% in 2003 and 74% in 2004. Among the reproductively mature geophytes, annual grasses and woody shrub species in the reserve, individuals were clearly distinguishable and their densities were determined from counts of the total numbers of individuals of each species present in each 100-m^2 experimental plot. In those plots where individual species densities substantially exceeded 500 individuals per 100 m^2, their densities were determined from counts of the average numbers of individuals present in 20 sub-plots (1-m^2 quadrats) randomized within each 100-m^2 plot. Among the reproductively mature perennial grasses in the reserve, individuals were indistinguishable and their abundances were determined from the average percentage covers of each species in 20 sub-plots (1-m^2 quadrats) randomized within each 100-m^2 plot.

Table 1. *F*-ratios from a three-way analysis of variance which tested the effects of different mechanical and chemical manipulations on the abundances of four different plant functional groups between two successive observation years differing in absolute amounts of annual precipitation in the Tienie Versfeld Wildflower Reserve.

Manipulations	Obligate seeders		Sprouters	
	Annual grasses	Forbs	Perennial grasses	Geophytes
Main effects				
Mechanical treatments	$\mathbf{F_{3,20} = 11.2}$***	$\mathbf{F_{3,20} = 6.9}$***	$\mathbf{F_{3,20} = 12.0}$***	$\mathbf{F_{3,20} = 2.8}$*
Chemical treatments	$\mathbf{F_{1,60} = 32.6}$***	$\mathbf{F_{1,60} = 23.1}$***	$F_{1,60} = 0.1$	$F_{1,60} = 0.1$
Observation year	$F_{1,60} = 2.1$	$\mathbf{F_{1,60} = 108.2}$***	$\mathbf{F_{1,60} = 98.6}$***	$\mathbf{F_{1,60} = 29.1}$***
Two-way interactions				
Mechanical × chemical treatments	$\mathbf{F_{3,60} = 3.1}$*	$F_{3,60} = 1.6$	$F_{3,60} = 0.8$	$F_{3,60} = 0.8$
Mechanical treatments × observation year	$F_{3,60} = 1.4$	$F_{3,60} = 1.7$	$F_{3,60} = 1.6$	$F_{3,60} = 1.1$
Chemical treatments × observation year	$\mathbf{F_{1,60} = 5.4}$*	$F_{1,60} = 0.2$	$F_{1,60} = 0.9$	$F_{1,60} = 0.1$
Three-way interactions				
Mechanical × chemical treatments ×observation year	$F_{3,60} = 0.8$	$F_{3,60} = 0.5$	$F_{3,60} = 0.6$	$F_{3,60} = 0.7$

*$P < 0.05$; ***$P < 0.001$.

Statistical analyses

The heterogeneous distributions of native and alien species in the experimental plots precluded statistical evaluation of their individual responses to the different mechanical and chemical manipulations applied. For this reason, species were clustered into larger functional groups based on their growth form (grass, herb or woody shrub) and recruitment strategy (obligate seeder or sprouter), the latter a crucial determinant of plant species persistence in the presence of regular disturbance. The obligate seeders constituted the annual grasses and forbs (therophytes). The sprouters comprised the perennial grasses and geophytes with subterranean vegetative propagating organs (stolons, bulbs, corms). Woody shrubs included both recruitment strategies.

A three-factor analysis of variance tested the main and interactive effects, of the mechanical and chemical manipulations applied, on the composition and abundance of the different functional groups between the two successive observation years receiving different amounts of annual precipitation. Woody shrubs were excluded from the statistical analyses owing to their sparse occurrence in the differently treated experimental plots. Percentage values were arcsine transformed to correct normality in proportions prior to statistical analysis. Significantly different treatment means were separated with a Duncan's Multiple Range test. Computed Pearson correlation coefficients and a Student's *t*-test evaluated statistical correspondence between measured abundances of the various functional groups.

Results

Functional group responses

The obligate seeding forbs comprised mainly the natives *Senecio littoreus* Thunb. (relative density 88%) and *Cotula filifolia* Thunb. (relative density 12%). Their total densities were significantly ($P \leq 0.001$) higher (5.0 times greater) in the wetter second year than the drier first, and significantly ($P \leq 0.001$) lower (1.9 times smaller) in plots that received the pre-emergent herbicide compared with those where the herbicide was excluded. Also, this functional group's densities were significantly ($P \leq 0.001$) altered in the differently mechanically manipulated plots (Table 1). General trends of increasing forb densities with increasing intensity of disturbance in the sequence mowed < lightly burnt < intensely burnt < hand-cleared were evident, both in those plots where the pre-emergent herbicide was added and in those where the herbicide was excluded, particularly in the wetter second observation year (Fig. 2A).

The obligate seeding annual grasses comprised principally the aliens *L. multiflorum, H. murinum, B. diandrus* and *A. fatua.* Their relative percentage densities of 69, 24, 5, and 2 in the first observation year were somewhat different from those of 78, 12, 8 and 2 in the second observation year due mainly to a significant ($P \leq 0.01$) reduction (2.1-fold decrease) in the fraction of the pioneer grass *H. murinum* ($F_{1,60} = 10.8$) in this functional group. Total densities of annual grasses did not differ significantly ($P \geq 0.05$) between the drier first and wetter second observation year (Table 1). They were significantly ($P \leq 0.001$) altered in the differently mechanically manipulated plots, with measured densities averaging between 4.9 and 5.5 times higher in the lightly burnt, intensely burnt, and hand-cleared plots than in the mowed plots. Also, densities of this functional group were significantly ($P \leq 0.001$) reduced in those plots where the pre-emergent herbicide was added (Table 1). However, significant ($P \leq 0.05$) interactions were evident between the mechanical and chemical treatments, and between chemical treatment and observation year (Table 1). The first interaction indicated that reductions in annual grass densities following addition of the pre-emergent herbicide (Fig. 2B) were larger in the lightly burnt plots (6.4-fold decrease) and mowed plots (4.0-fold decrease) than in the intensely burnt plots (2.7-fold decrease) and hand-cleared plots (1.4-fold decrease). The second interaction specified greater herbicide-induced reductions in total densities of annual grasses (Fig. 2B) in the drier first observation year (6.6-fold decrease) than the wetter second (1.7-fold decrease).

The sprouting geophytes comprised predominantly the natives *Ornitholgalum conicum* Jacq. and *O. thyrsoides* Jacq. (combined relative density 72%), *Romulea tabularis* Eckl. ex Beg. (relative density 15%), *Trachyandra revoluta* (L.) Kunth, *Babiana angustifolia* Sweet, *Zantedeschia aethiopica* (L.) Spreng (combined relative density 10%) and *Ammocharis coranica* (Ker Gawl.) Herb., *Geissorhiza aspera* Goldblatt, *Chlorophytum triflorum* (Aiton) Kunth, and *Ixia maculata,* L. (combined relative density 5%). Their total densities were not significantly ($P \geq 0.05$) affected by the addition of the pre-emergent herbicide (Table 1). However, densities of this functional group were significantly ($P \leq 0.001$) higher (3.4 times greater) in the wetter second year than the drier first. Also, they were significantly ($P \leq 0.05$) altered in the differently mechanically manipulated plots with a significant interaction ($P \leq 0.05$) evident between mechanical treatment and observation year (Table 1). This interaction indicated larger increases in geophyte densities between the drier first and wetter second observation year (Fig. 3A) in the mowed plots (10.5-fold increase) than in the hand-cleared plots (7.9-fold increase), intensely burnt plots (3.9-fold increase) and lightly burnt plots (1.6-fold increase)

The sprouting perennial grasses comprised primarily the native *Sporobolus virginicus* (L.) Kunth (relative cover 40%) and the alien *C. dactylon* (relative cover 60%) of subtropical origin. The relative densities of the native and alien perennial grasses in this functional group were not significantly ($P \geq 0.05$) affected by the higher annual precipitation in the second observation year ($F_{1,60} = 0.2$), by any of the mechanical manipulations applied ($F_{3,20} = 1.6$), or by the addition of the pre-emergent herbicide ($F_{1,60} = 0.1$). Total covers of perennial grasses were signifi-

cantly ($P \leq 0.001$) lower (2.3 times smaller) in the wetter second than in drier first observation year (Table 1) but were not significantly ($P \geq 0.05$) affected by the addition of the pre-emergent herbicide (Table 1). However, covers of this functional group did differ significantly ($P \leq 0.01$) between the differently mechanically manipulated plots, the measured amounts in the lightly burnt plots being consistently higher (up to 3.8 times more) than those in the mowed, hand-cleared and intensely burnt plots (Fig. 3B).

Functional group associations

Total densities of forbs were positively correlated ($P \leq 0.01$) with those of annual grasses and also with those of geophytes (Table 2). Total covers of perennial grasses were negatively correlated ($P \leq 0.05$) with total densities of geophytes and also with those of forbs, but were not significantly correlated ($P \geq 0.05$) with those of annual grasses.

Expenditure

Expenditure on labour, including direct supervision, transport and administration costs incurred by the contractor, on capital equipment including protective clothing (capital outlay adjusted for a guaranteed one year life span), and on consumables are summarized for the different mechanical and chemical manipulations in Table 3. Total clearing costs were in the sequence herbicide application > hand-clearing > light intensity burning > mowing > intense burning. Costs associated with intense burning of uncut grass (R415/ha), grass mowing (R924/ha) and light intensity burning of mowed grass (R1338/ha) were all less than those (up to R1927/ha) reported for clearing dense stands of woody aliens. However, costs of hand-clearing of grass (R6743/ha) and pre-emergent herbicide application (R13 380/ha) were much greater.

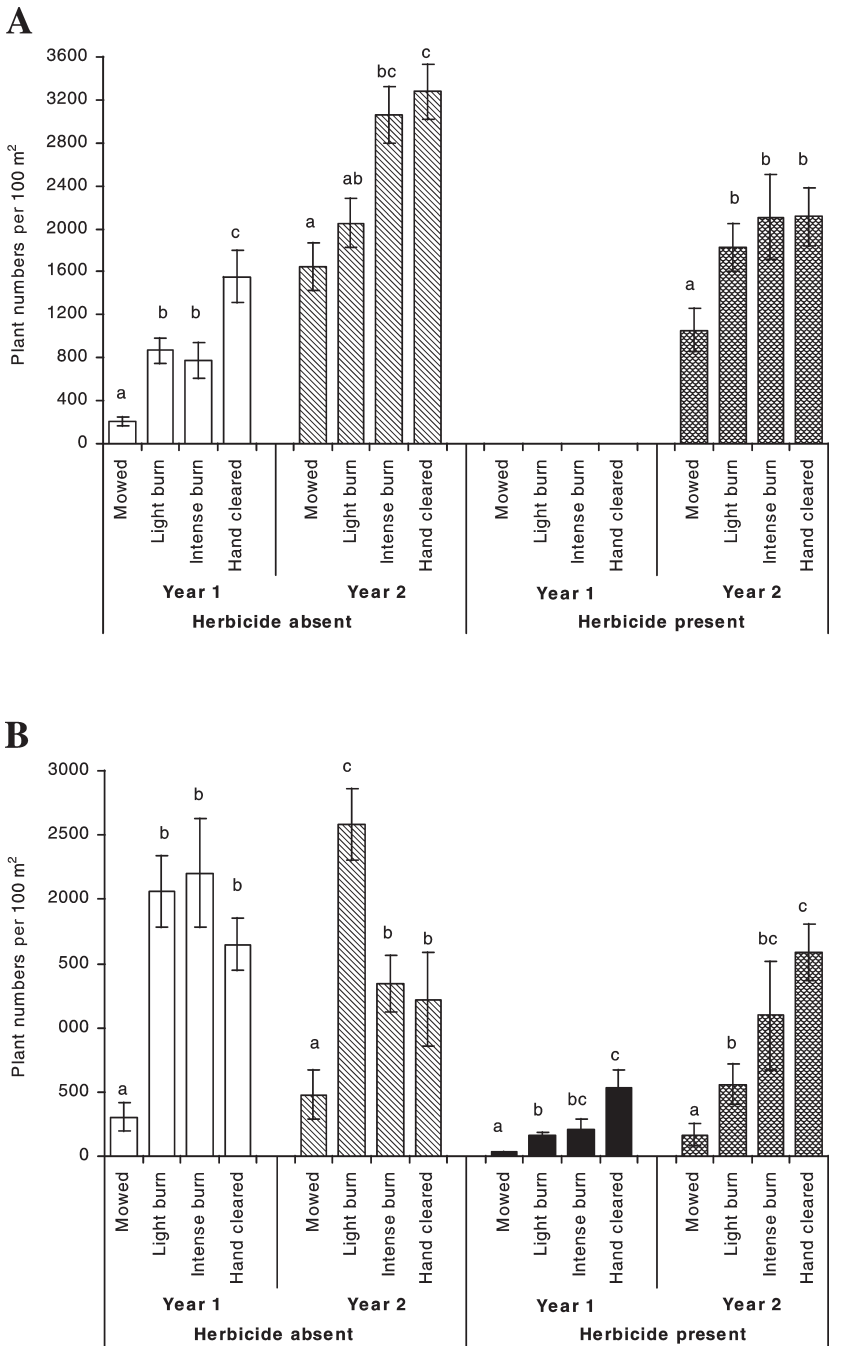

Fig. 2. Average densities ± standard errors of obligate seeders (**A**) forbs and (**B**) annual grasses in differently mechanically and chemically manipulated plots between two successive observation years differing in absolute amounts of annual precipitation (2003: 302 mm; 2004: 439 mm). Bars with different letters (a, b, c) are significantly different ($P < 0.05$).

Discussion

The intense burning of uncut vegetation provided the cheapest strategy overall for managing the invasive annual grasses in renosterveld, which is considered naturally adapted to fire,[21,22] though intense and frequent fires tend to reduce species richness of this flora.[15] This strategy, which elicited responses from the four functional groups of similar magnitude as the much more expensive hand-clearing treatment, stimulated recruitment of forbs, annual and perennial grasses. Its limitation was that it inhibited recruitment of geophytes, this most evident in the wetter second observation

Table 2. Statistical correspondence between measured abundances of four different plant functional groups.

	Annual grasses		Perennial grasses		Forbs	
	Pearson coefficient	*t*-statistic	Pearson coefficient	*t*-statistic	Pearson coefficient	*t*-statistic
Perennial grasses	$r = 0.022$	$t_{1,94} = 0.215$				
Forbs	$r = 0.277$	$\mathbf{t_{1,94} = 2.784}$**	$r = -0.405$	$\mathbf{t_{1,94} = -4.271}$***		
Geophytes	$r = 0.009$	$t_{1,94} = 0.086$	$r = -0.198$	$\mathbf{t_{1,94} = -1.952}$*	$r = 0.265$	$\mathbf{t_{1,94} = 2.645}$**

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

year (Fig. 3A). By contrast, the slightly more expensive light intensity burn, which involved burning of mowed grass, also stimulated recruitment of sprouting geophytes. Burning and clearing, like other forms of disturbance,[4,24–26] are known to favour the germination and establishment of invasive annual grasses, including *Lolium multiflorum,* and this has been attributed to an increase in the ratio of short- to long-wave radiation reaching seeds on the soil surface.[22] Also, fire is known to alter soil mineral levels,[27] especially nitrogen and phosphorus in arid regions,[24] and rates of water infiltration into soils,[28–31] these factors possibly contributing to the greater recruitment of invasive annual grasses observed in the burnt plots in this study. Indeed, the establishment and growth of invasive annual grasses is known to be enhanced by soil nitrogen enrichment[32] and supplemental water.[33] Also, invasive annual grasses such as *Bromus rubens* L., *B. tectorum* L. and *Schismus barbatus* (Loefl. exL) Thellung have been reported to utilize elevated soil N levels more rapidly and to compete for soil water resources more effectively than native species,[34,35] thereby reducing native seedling biomass and species richness.[17]

The generally positive interactions reported between invasive annual grass establishment and fire suggest that the control of invasive annual grasses by burning may be effective only if all adult plants and their vegetative propagating organs are destroyed and their seed banks eliminated.[36] In this regard, it has been reported that the invasive annual grass *Bromus tectorum* L. is particularly amenable to control by fire prior to seed dispersal, since its soil seed bank can approach zeroat this stage.[37] However, the effectiveness of fire in controlling other invasive annual grasses has been reported as only partial or temporary, with inadequate information regarding seed longevity often leading to incorrect management recommendations.[38] For example, fire was initially proposed for the control of the invasive annual grass *Taeniatherum caput*-medusae (L.) Nevski,[39] but later studies demonstrated that its effectiveness was incomplete,[40] requiring follow-up treatment with propane weed flamers to destroy individuals that escaped initial fire treatments.[41] This technique, along with herbicide applications and grazing, has recently been considered for restoration work in sagebrush annual grassland communities in the Great Basin area in the United States.[42]

Grazing by cattle and sheep during

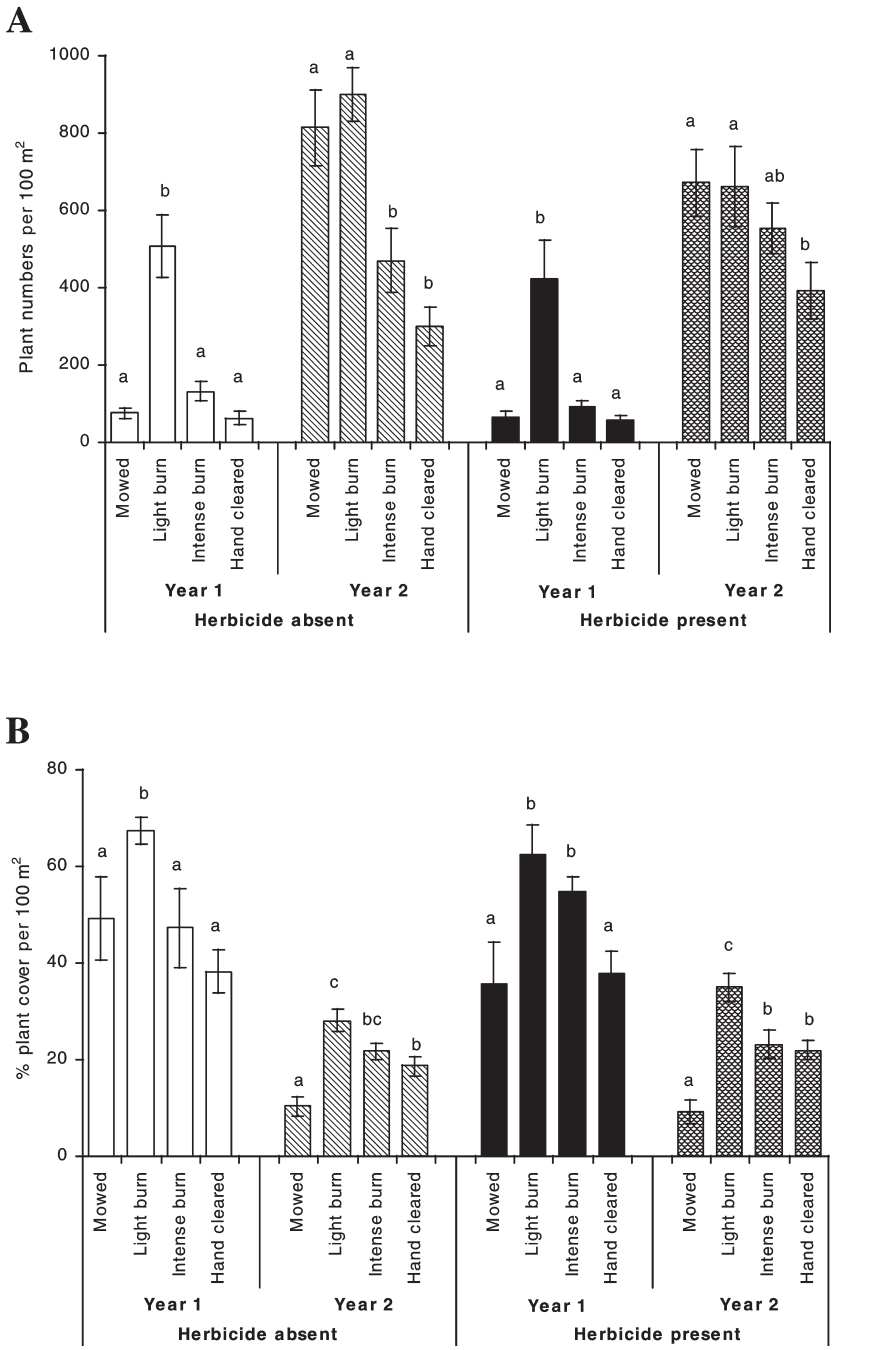

Fig. 3. Average covers ± standard errors of sprouters (**A**) geophytes and (**B**) perennial grasses in differently mechanically and chemically manipulated plots between two successive observation years differing in absolute amounts of annual precipitation (2003: 302 mm; 2004: 439 mm). Bars with different letters (a, b, c) are significantly different ($P < 0.05$).

Table 3. Expenditure on different mechanical and chemical manipulations applied in the Tienie Versfeld Wildflower Reserve.

Manipulation	Expenditure per ha (R†)			
	Labour	Capital equipment	Consumables	Total
Mechanical				
Mowing	372	132*	419	924
Light burn	663	215*	460	1 338
Intense burn	290	83	41	415
Hand-clearing	6 738	5*	–	6 743
Chemical				
Pre-emergent herbicide	154	11	13 215	13 380

*Expenditure on capital equipment adjusted for duration of equipment usage as a fraction of its 12-month guaranteed life span. This was calculated as total capital equipment cost × (14 contract working-days/260 working-days per year).
†1US$ = R6.70.

flowering and seed set of annual grasses has been used to control annual grass weeds in Australia and South Africa. The advantage is that costs are low. The disadvantages include avoidance by such ungulates of invasive annual grasses with sharp unpalatable seeds, such as *Vulpia, Hordeum* and *Bromus.* This leads to their increase[16,43] while the more palatable invasive annual grasses, e.g. *Lolium* and *Avena,* decrease,[43] as do palatable perennial grasses indigenous to renosterveld.[22,44] Another disadvantage is that ungulate grazing intensity needs to be high to reduce seed production. Indeed, intensive ungulate grazing and associated trampling and dunging are considered incompatible with conservation of native plant diversity in renosterveld because this promotes invasive annual plants as well as 'weedy' indigenous geophytes,[15] such as the cincherinchees (*O. conicum* and *O. thyrsioides*), which are particularly toxic to livestock.[45] Paradoxically, ungulate grazing has proved a highly effective tool for reducing grass fuel loads and risk of catastrophic fires in other ecosystems,[46,47] yet continued grazing inevitably leads to reductions in native species cover and diversity. Indeed, the ecological effects of ungulate grazing on ecosystems around the world continue to inspire fervent debate.[48–51] Ungulate exclusion from ecosystems that have evolved in their absence has proved an ecologically and economically cost-effective restoration strategy, across large areas and diverse ecological communities. However, there are few data on the effects of ungulate grazing on native species cover and diversity in renosterveld. Preliminary studies have reported that intensive grazing has little effect on species richness as a whole but alters renosterveld composition by causing a reduction in perennial grasses, and an increase in certain geophytes and Asteraceous shrubs.[44]

The mowing treatment, which was slightly less expensive than the light intensity burn (Table 3), elicited responses of the smallest magnitude from the four designated functional groups. This was most apparent in the first observation year, when measured densities of especially the obligate seeding annual grasses and forbs in the mowed plots were substantially smaller than those in the hand-cleared, lightly and intensely burnt plots. These lower recruitment levels in the mowed plots concurred with reports that plants, particularly those with smaller seeds, have greater difficulty in emerging from the dense litter layer produced by invasive annual grasses due to insufficient light and seed resources.[52–55] In fact, the dense litter produced by invasive annual grasses is known to inhibit the germination and establishment of native taxa[6,53,54] and to alter soil moisture and temperature regimes that promote fungal pathogens[56] and other seed and seedling predators.[57] Noteworthy also was the considerably increased densities of native forbs and geophytes in the mowed plots in the second observation year, their measured densities approaching those in the lightly burnt plots, whereas those of the invasive annual grasses remained at levels similar to those in the drier first observation year. Conversely, covers of creeping perennial grasses in the mowed plots were reduced in the second observation year to levels below those measured in the first, the reduced cover presumably contributing to the enhanced recruitment of the forbs and geophytes. Indeed, the cover of perennial grasses in this study was negatively correlated with the densities of annual forbs and geophytes, but not with those of the annual grasses, despite reports that high densities of annual grasses may prohibit perennial grass establishment.[58] Persistent, creeping perennial grasses, such as *Cynodon dactylon,* are known to exclude the establishment of shrubs[59] and tussock grasses, particularly where grazers and browsers are present.[60] Their dense root systems intensify below-ground competition, which restrains the growth of some invasive annual grasses, such *Bromus tectorum,*[61] and inhibits nutrient and water acquisition by native species, reducing their growth and reproductive output.[33,62,63]

The application of the pre-emergence herbicide appeared to be the most effective, though most expensive, method (Table 3) for controlling the invasive annual grasses over the short term. The effectiveness of this herbicide was greatest in the first observation year and in the lightly burnt plots, though its effectiveness did persist with diminished intensity in the differently mechanically manipulated plots in the second year. This treatment's disadvantage was that it simultaneously inhibited recruitment of native species of forbs, though it did not detrimentally influence springtime densities of perennial grasses or indigenous geophytes. This was expected as such herbicides kill germinating seeds rather than established sprouting plants. Another short-term disadvantage of herbicide application is that inhibition of annual grass populations does not necessarily result in greatly decreased seed production or reduced rates of seed bank accumulation.[43] Penetration of trifluralin, an active ingredient of pre-emergent herbicides, into un-tilled soils has been reported as poor.[64] Of particular concern, however, is the reported rapid development of multiple herbicide resistance among especially annual hybrids of *Lolium* in South Africa, which implies that chemical control measures may become less cost effective with repeated herbicide use.[65,66]

Conclusions

We conclude that the mowing of grass-infested renosterveld prior to grass seed maturation, and removal of the cut grass biomass for use as fodder in restricted feed lots to offset clearing costs, provides the most credible strategy for controlling the annual grass populations to conserve native floral diversity over the short term. However, at sites where invasive annual grass infestations are exceptionally heavy and have persisted for many years, an initial light intensity autumn burn to remove excessive grass litter, and to promote flowering, seed production and smoke-stimulated germination of native taxa,[67] followed by the addition of a pre-emergent herbicide to limit subsequent recruitment of invasive annual grasses, may assist in partly recovering native floral diversity. In such cases, the net effects of smoke-stimulated vs herbicide-inhibited germination of newly fallen seeds of indigenous shrubs, forbs and geophytes requires testing. However, effective long-term control of invasive annual grasses will most likely be realized by an integrated management approach that seeks to limit factors which promote their success, for instance soil N enrichment and intensive disturbance, and apply strategies that reduce seed production and seed accumulation. Sucrose has been used experimentally to reduce available nitrogen by increasing soil microbial biomass. Such treatments have reduced the growth of invasive plants while enhancing the establishment and composition of late-seral native plants in a semi-arid ecosystem.[68,69] Other strategies that may reduce growth and seed production in the invasive annual grasses include the introduction of species-specific pathogens,[70] and the identification and use of competitive native species that can successfully germinate and establish in the presence of the invasive annuals.[71] Indeed, restoration projects that involve the mixing of native species to provide a variety of above- and below-ground growth forms, and their sowing

at high densities, may increase the establishment of desirable plants while also providing adequate competition against invasive plants.[37]

For vegetation in the densely populated and intensively farmed Western Cape lowlands, the days of hands-off conservation are over. This reality can be viewed both as a threat to the persistence of species and an opportunity for job creation. Given the highly fragmented and degraded condition of renosterveld throughout the Cape Floral Region, successful restoration projects of even a few hectares, particularly at sites with short histories of agricultural intensification which have the greatest recovery potential,[72] could create urgently needed new habitats for subsequent rare species recovery and/or introductions. These would serve a much needed propagule source and catalyst for future larger-scale projects. The invasion of disturbed and nutrient-enriched vegetation fragments by weeds is continuous and chronic. Budgets for regular monitoring and labour-intensive management of these fragments will be essential if they are to serve this purpose. Regardless of the specific techniques employed, the costs per unit area should decrease, and the effectiveness of the treatments should increase as economies of scale are realized.[73]

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